

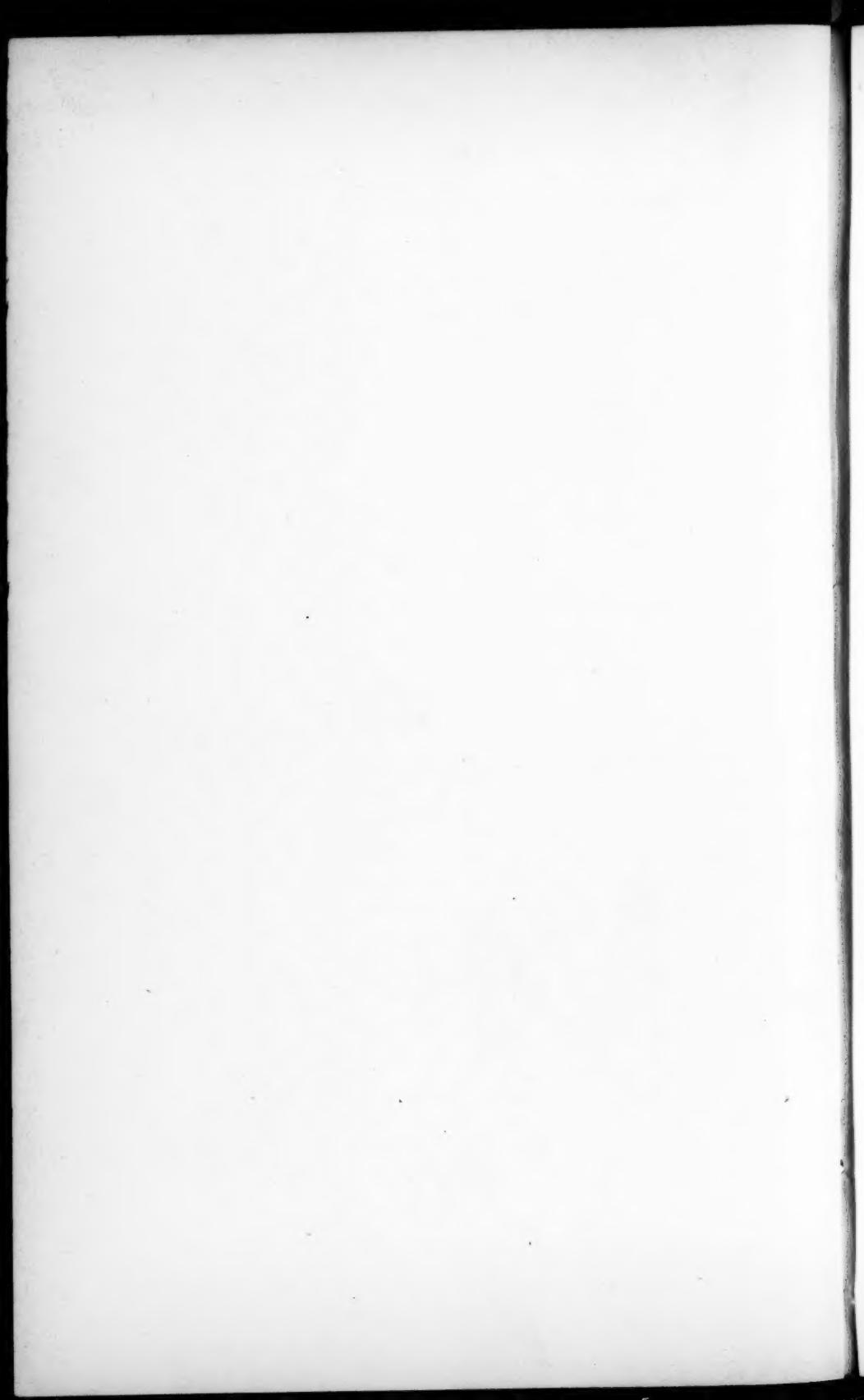
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CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE
MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE.
E. L. MARK, DIRECTOR.—No. 146.

*THE LAWS OF HEREDITY OF GALTON AND MENDEL,
AND SOME LAWS GOVERNING RACE
IMPROVEMENT BY SELECTION.*

BY W. E. CASTLE.



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I. THE "LAW OF ANCESTRAL HEREDITY."

IN the year 1889, the eminent English statistician, Francis Galton, attempted to give precise mathematical expression to the well-known fact that the child resembles in varying degree its ancestors near and remote. From a study of family statistics of stature, he found that children resemble their parents, on the average, more closely than their grandparents, and the latter more closely than their great-grandparents, and so on to ancestors still more remote. He tentatively advanced the hypothesis that the resemblance to each earlier generation of ancestors is just half that to the next later.

Galton subsequently tested this hypothesis in the case of a domesticated animal, by applying it to an extensive series of records of the inheritance of black spots in Basset hounds. Satisfied with the result, Galton ('97, p. 502) then formulated as follows the general "Law of Ancestral Heredity":—"The two parents contribute between them, on the average one-half, or (0.5) of the total heritage of the offspring; the four grandparents, one-quarter, or $(0.5)^2$; the eight great-grandparents, one-eighth, or $(0.5)^3$, and so on. Thus the sum of the ancestral contri-

butions is expressed by the series $[(0.5) + (0.5)^2 + (0.5)^3$, etc.], which, being equal to 1, accounts for the whole heritage." Galton found that, allowance being made for male prepotency, the theoretical values calculated in accordance with this "law" conform very closely to the values actually observed in the series of generations of Basset hounds. He, therefore, put his law forward as a general law of ancestral heredity.

But subsequent examination by Pearson ('98) of the material studied by Galton, and of other material similar in nature, has failed to substantiate Galton's conclusion, except in a much modified form. In the most recent statement of his views, Pearson (:03) holds with Galton that the best prediction as to the character of the offspring must be based upon the character of the ancestors, and that the influence of the various ancestors diminishes as they become more remote. He believes that "the contributions of the ancestry follow a geometrical series, although not that originally proposed by Mr. Galton." From a study of the inheritance of eye-color in man and coat-color in thoroughbred horses, he concludes that "as far as the available data at present go, inheritance coefficients for ascending ancestry are within the limits of observational error represented by a geometrical series and by the same series." This series, he observes, approximates those designated I and II below: —

	Pearson's Series I.	Pearson's Series II.	Galton's Series.
Parental influence49	.50	.50
Grandparental influence32	.33	.25
Great-grandparental influence20	.22	.125
Great-great-grandparental influence13	.15	.0625

Comparing Pearson's series with that of Galton, we see that the parental influence is reckoned as substantially the same by both Galton and Pearson, but that Pearson assigns a much greater influence to the more remote ancestors than does Galton.

It should be observed that the "available data" upon which principally Pearson bases his conclusions consist of two cases of pigment inheritance, one in man, the other in the horse. A third well-known series of this sort has not been utilized by Pearson, though our information about it is much more complete and precise than that about either of the other two. I refer to the statistics about color inheritance in mice recorded by von Guaita ('98, :00), of which an analysis has been made by Davenport (:00). In this series the inheritance of

color follows closely neither the law of Galton nor the series suggested by Pearson.

The lack of agreement in this case with Galton's law has been pointed out by Davenport for certain of the color categories. He concludes that in the case of gray alone does the color inheritance among von Guaita's mice conform closely with Galton's law. But in reality, even in the case of gray, close agreement does not occur; Davenport's conclusion that it does occur results from the inclusion by him in a single color category of two sorts of mice which are clearly quite distinct, namely, (1) mice gray all over like the wild house-mice, and (2) gray mice with white markings. Even when these two categories are combined, Davenport's figures show close agreement between the observed and calculated numbers in two only of the five filial generations with which he deals, namely, in the third and sixth generations (of von Guaita's nomenclature), in which he finds observed and calculated to agree perfectly. But in the three remaining generations he finds observed and calculated percentages to be related as follows:—

Generation	II.	IV.	V.
Observed	100 %	58 %	48 %
Calculated	0 %	48 %	60 %

Davenport, moreover, has excluded from the category of "albinos" white mice which possess the dancing character. But this is manifestly an error, for the dancing character has nothing to do with coat-color, and is inherited quite independently of it. Davenport's classification, accordingly, makes the category of albinos appear smaller than it really is. If we include all albinos (whether dancers or not) in one category, and make separate classes for gray, gray-white, black, and black-white mice, the relations between the observed and calculated numbers in each generation are found to be as indicated in Table I, Davenport's method of calculation being followed.

An examination of this table shows no close agreement between calculated and observed conditions throughout any single category or any single generation, although the totals turn out better than the predictions for the generations considered separately. In Generation II the discrepancies are glaring. In the column, white, the grand totals alone agree closely, yet this agreement is clearly without significance; it is a chance agreement in the totals of two series divergent throughout.

The observed numbers, it is evident, agree no better with one of Pearson's series than with that of Galton. The discrepancies noted

TABLE I.

TEST OF GALTON'S LAW BY THE STATISTICS OF VON GUAITA.

B, black; *B-W*, black-white; *G*, gray; *G-W*, gray-white; *W*, white.

Generation.		<i>G.</i>	<i>G-W.</i>	<i>B.</i>	<i>B-W.</i>	<i>W.</i>	Total.
II.	Calc.	0			14	14	
	Obs.	28			0	0	28
III.	Calc.	22	0	0	11	11	
	Obs.	17	8	4	1	14	44
IV.	Calc.	14	1	0	3.8	12.1	
	Obs.	16	5	4	1	5	31
V.	Calc.	23	45	13.7	16	15.5	
	Obs.	3	55	12	24	19	113
VI.	Calc.	10.5	31.2	18.4	6	20.4	
	Obs.	2	22	9	17	36	86
VII.	Calc.	1.2	1	0.7	0.2	8.7	
	Obs.	0	4	0	0	3	7
Total	Calc.	70.7	78	32.8	51	76.7	
	Obs.	66	94	29	43	77	309
Ratio, Obs. : Calc.		93.3 %	120.5 %	88.4 %	84.8 %	100+ %	

between observed and calculated will remain and even be accentuated if we replace Galton's series with one of those suggested by Pearson. For the result will be unchanged in Generation II, but the calculated numbers will in most cases diverge still more from the observed ones, in the later generations, because Pearson attaches more weight to the remoter ancestors than does Galton.

It is evident, then, that some fundamental defect exists in the "law of ancestral heredity," as stated by either Galton or Pearson. It fails in the case just examined not only to account for the observed result, but

even to enable one to predict that result with any degree of accuracy, and that too in the very category of cases which it was originally formulated to cover, namely in color inheritance among mammals. Galton himself (97, p. 403) recognized the existence of such a defect, though he considered it, for practical purposes, of little consequence. Stated in his own words it is as follows:—

"The chief line of descent," it is generally believed, "runs from germ to germ and not from person to person." Yet "the person may be accepted on the whole as a fair representative of the germ, and, being so, the statistical laws which apply to persons would apply to the germs also, though with less precision in individual cases." Failure of Galton's law in the case of von Guaita's statistics is due to the falsity of the assumption here made by Galton that the person is "a fair representative of the germ." In all cases of alternative inheritance the person (or soma) represents only a *part* of the ripe germs produced by the individual, in some cases it may even represent none of them. Hence any theory of heredity which bases its predictions as to the character of the offspring solely upon the character of the soma of the ancestors, is clearly inapplicable to cases of alternative inheritance. The presumption is against its application to any other class of cases until that applicability has been demonstrated.

II. MENDEL'S LAW OF HEREDITY.

Certain facts of alternative inheritance were clearly stated and accounted for many years ago by Gregor Mendel (66). He thus not only formulated laws of alternative inheritance, whose correctness has been fully confirmed by a number of independent observations, but he also laid the foundation for a general theory of heredity. In the history of the study of heredity his discovery is the most fundamental and far-reaching. Its importance is not lessened by the fact that it was long unrecognized. Only under the fertilizing influence of Weismann's ideas was the rediscovery of Mendel's law accomplished independently by de Vries (60), Correns (60), Tschermak (60), and others. To its further development no one has contributed more than Bateson (62).

Where Galton's law gives us at best rough approximations based upon averages of heterogeneous material, and with no attempt at an explanation of the results, Mendel's law enables us to make predictions for specific cases as to both the character and the numerical proportions of the offspring to be expected, and furnishes us at the same time with a

rational explanation of the outcome. It thus meets the two-fold requirements of a scientific theory, a statement of phenomena and an explanation of them; the "law of ancestral heredity" attempts only the first of these two things, and even here fails lamentably. It will thus be seen that the claims of Mendel's law are much greater than those of Galton's law. If it fails, its failure is as much more signal.

The same test may be applied to Mendel's law as to Galton's. Can we, on the basis of Mendel's law, make predictions concerning the various generations of von Guaita's mice with greater accuracy than has been found possible under Galton's law? Before we can frame an answer to this question, we must know precisely what the Mendelian predictions are.

Mendelian predictions are based, not on the *somatic character of the parents*, but on the character of the *germ-cells* formed by the parents. The simplest way of determining the character of the germ-cells formed by an animal or plant is by experimental breeding tests. In cases where this is not practicable, one can often predict with equal confidence from a knowledge concerning the grandparents, not as to their *somatic character*, but as to the character of their *germ-cells* as evidenced by the nature of the offspring produced by them. Stated in the terminology of present-day biology, the principles which underlie the Mendelian predictions are these: —

1. Every gamete (egg or spermatozoon) bears the determinants of a complete set of somatic characters of the species. Accordingly when two gametes (an egg and a spermatozoon) have met in fertilization, there are present in the fertilized egg the representatives of *two sets* of somatic characters, which may or may not be the same. If they are the same for a given character, as, for example, coat-color in mammals, the individual which develops from the egg must inevitably have that same character. Thus when gametes formed by one white mouse meet in fertilization gametes formed by another white mouse, the offspring are invariably white. Similarly when a wild gray mouse is bred to another wild gray mouse the offspring are invariably gray. And when a pure-bred spotted black-white mouse is bred to a mouse like itself, the offspring are all spotted black-white.

2. But when the two gametes uniting bear each what represents a *different* somatic character, only one of these characters may be manifested by the individual (or zygote) formed. Thus, when wild gray mice are mated with white mice, only gray offspring are produced. The gray character is, in Mendel's terminology, *dominant*, the white character

recessive. Or, when wild gray rats are mated with black-white rats, only gray rats are produced. The wild gray character is, accordingly, dominant not only over white, but also over black-white.

3. Sometimes the zygote formed by the union of two unlike gametes (heterozygote, Bateson, :o) develops the character of neither parent in its purity. It may have a character intermediate between those of its parents, or something entirely different from either. Thus when black-white mice are mated with white mice, the offspring are gray like the wild house mouse.

4. Whatever the somatic character of the zygote is, the germ-cells which it forms will be, in respect to any particular character, like those which united to produce it,—half like the maternal and half like the paternal gamete. Thus, a gray mouse obtained by crossing a wild gray mouse with a white one forms in equal numbers gametes which bear the gray character and those which bear the white character. This is conclusively shown by two simple breeding tests: 1) when a cross-bred (or hybrid) gray mouse is bred to a white mouse, half the offspring are hybrid grays, half are white. This is precisely the result we should expect if the cross-bred gray mouse forms, in equal numbers, as we have supposed, gametes which bear the gray and those which bear the white character. For

The gray mouse will produce gametes	<i>G</i> and <i>W</i>
The white mouse, gametes	<i>W</i> and <i>W</i>
And the possible combinations of these 2 sets are their product	$\frac{2\,GW + 2\,WW}{}$

But, as we have already stated, when a zygote contains *both* the gray character and the white character, only the former will be visible. This may be indicated by placing the (invisible) *W* within a parenthesis. Further, in the expression $2\,WW$ one of the identical letters may be dropped as superfluous. Our formula, representing the outcome of the breeding test described, then reads $2\,G(W) + 2\,W$, and signifies that two in every four of the offspring produced will be gray hybrids, and the remaining two white. 2) When two cross-bred (or hybrid) gray mice are bred together, the offspring consist of gray mice and white mice in the ratio of three gray to one white. Moreover, breeding tests show that of the three gray mice thus obtained one is pure, that is, will form only gametes bearing the gray character, while two are hybrid, that is, will form gametes some of which bear the gray character, others the white character. This is precisely the result expected under our hypothesis that each hybrid individual forms gametes *G* and *W* in equal numbers.

For the possible combinations of two sets of gametes each *G* and *W* are represented by their product $GG + 2GW + WW$, or simplified as already explained, $G + 2G(W) + W$.

The principle illustrated by these examples is, as pointed out by Bateson (:02), the most fundamental and far-reaching of the Mendelian ideas. It is known as the law of segregation, or "splitting" (de Vries, :00) of the parental characters at gamete formation, or as the "principle of gametic purity" (Bateson, :02). Dominance is purely a secondary matter; it may or may not occur along with segregation, though the latter can be more easily demonstrated in cases where it is associated with the former. The principle of gametic purity just stated rests upon the assumption that gamete-formation is the reverse of fertilization. In fertilization, gametes *A* and *B* unite to form a zygote *AB*; when this zygote in turn forms gametes, they will be again *A* and *B*. From a knowledge of the *somatic form* alone of pure *As* and *Bs*, one can make no trustworthy prediction as to the form of *AB*.—Here is the fundamental error of the "law of ancestral heredity" as stated by Galton ('97) or Pearson (:03).—*AB* may have invariably the somatic form of *A* or of *B* (cases of simple dominance, as of gray over white in mice); or it may have *sometimes* the form of *A*, sometimes that of *B* (cases of alternative dominance—see Tschermark (:02)—); or, finally, the somatic form of *AB* may be different from both that of *A* and that of *B* (cases like that of the gray hybrid formed by the cross of black-white with white mice). But, no matter what the somatic form of *AB* is, we may with confidence predict that its gametes will be essentially pure *As* and pure *Bs*, and the two will be produced in proportions approximately equal. This is the Mendelian expectation in all cases of alternative inheritance. Whether it applies to other cases also, and if so to what extent, is not yet known. For the present we may confine our attention to the case which afforded a basis for the "law of ancestral heredity," namely alternative color-inheritance among mammals.

In Table II are given the Mendelian predictions for the inheritance of complete albinism in the various generations and matings of von Guaita's mice. These predictions are based upon the fact repeatedly observed that complete albinism behaves as a *recessive* character in heredity with reference to a pigmented character of any sort (gray, black, or spotted). Predictions are not made for the other color categories separately, because their relations to each other are not entirely clear from von Guaita's experiments. It seems probable, however, that they bear one toward another relations of alternative dominance. This

TABLE II.

TEST OF MENDEL'S LAW BY VON GUAITA'S STATISTICS.

Abbreviations as in Table I.

Generation	Pair.	Total Young.	Mendel's Law, Calc. No. W .	Observed No. W .	Galton's Law, Calc. No. W .
II.		28	0	0	14
III.		44	11	14	11
IV.	(1)	4	4	4	2.5
	(2)	16	0	0	6
	(3)	2	0	0	0.25
	(4)	7	0	0	2.62
	(5)	2	1	1	0.75
	Total	31	5	5	12.12
V.	(1)	16	0	0	1
	(2)	5	1.2+	2	1
	(3)	32	8	7	6
	(4)	13	0	0	1.6
	(5)	44	11	9	5.5
	(6)	3	0.7+	1	0.4
	Total	113	21	19	15.5
VI.	(1)	32	8	10	2
	(2)	6	6	6	4
	(3)	43	21.5	20	14
	(4)	2	0?	0	0.2
	(5)	3	0?	0	0.2
	Total	86	35.5	36	20.4
VII.	(1)	4	0	0	1.4
	(2)	3	3	3	2.3
	Total	7	3	3	3.7
	Total . . .	309	75.5	77	76.7

matter is now undergoing experimental tests which, when complete, may enable us to make predictions for these color categories not less precise than those given for white.

In the last column of the table are given for comparison the predictions based on Galton's law for the corresponding generations and pairs. If we were to consider the grand totals only, we might conclude that the Galtonian predictions are quite as good as the Mendelian, but if we examine item by item the two series from which these totals are made up, we see that there is no comparison in point of accuracy between the two sets of predictions. The Mendelian predictions are very close to the observed numbers throughout the table, generation by generation and pair by pair. In all cases except four the predictions are either perfect or within one of perfection, and in one only of these cases is the error greater than two. This one case is the total for generation III where the observed number is fourteen, the expectation eleven. Rarely do the Galtonian predictions come within one, or anywhere near one, of perfection. They demand the occurrence of white individuals in every generation and among the offspring of nearly every pair in the series, whereas white individuals are entirely wanting, and according to Mendel's law are not to be expected, among the offspring of *all* pairs in the second generation, and of eight other pairs in later generations of the series. The test is conclusive in favor of Mendel's law and against the "law of ancestral heredity," in the special case of albinism in mice. Elsewhere Castle and Allen (:03) have shown that among organisms in general albinism probably follows the same (Mendelian) law of inheritance.

Numerous other cases of Mendelian inheritance covering a wide range of characters are recorded in recent papers by de Vries (:01-03), Correns (:01, :03), Tschermak (:01, :01^a, :02), Bateson and Saunders (:02), Webber (:00), Spillman (:02, :02^a), Hurst (:02, :03), and others. These cases show that the Mendelian laws are widely applicable. They are not laws of hybridization merely, as Vernon (:03) and some others assume, but are general laws of alternative inheritance.

III. YULE ON GALTON'S LAW AND MENDEL'S LAW.

Bateson (:02) has taken the very reasonable position that Mendel's law and the law of "ancestral heredity" cannot both be applicable to the same classes of cases. But Yule (:02) sees no incompatibility between the two, and this view Pearson (:03) endorses. Yule says (p. 226),

"Mendel's Laws, so far from being in any way inconsistent with the Law of Ancestral Heredity, lead then directly to a special case of that law, for the *dominant* attribute at least. For the *recessive* attribute it does not hold." Let us see how Yule reaches this curious conclusion, that certain Mendelian predictions are only a special category of the more general predictions of the law of ancestral heredity.

After a statement of the Galton-Pearson law, whereby it is limited to no particular series, geometrical or otherwise, but is made to include any set of empirical averages of the characters of the ancestors, which can be made the basis of predictions, he proceeds as follows: "The first question to be asked is one that does not seem to have occurred to any of Mendel's followers, viz.: what, exactly, happens if the two races *A* [dominants] and *a* [recessives] are left to themselves to inter-cross freely *as if they were one race?*" In answer to this question, Yule draws the correct conclusion that the first cross-bred (or hybrid) generation will consist exclusively of dominants, but that all subsequent generations will consist of dominant and recessive individuals in the proportions, 3 dominant: 1 recessive, [provided no selection is practised and all individuals are equally fertile]. Yule next inquires, if I understand him rightly, what will be the effect of eliminating in each generation *all the recessive individuals*. Starting with 300 dominant individuals, which are in the Mendelian proportions, 100 pure: 200 hybrid, he finds that the successive generations will contain the following proportions of dominant individuals: —

.83333
.85000
.85294
.85345
.85354

He considers it useless to carry the series farther, as it "tends toward the limiting value .85355339 . . ." Now, what, in plain unmathematical language, does this mean? It means that when a dominant form has once been crossed with a recessive (as a pigmented animal, for example, with an albino), the stock of the former is forever contaminated, and cannot be freed entirely from the albino character by mere elimination of white individuals, however long the process is continued. Ever afterward the cross-bred dominant stock will produce on the average at least fourteen or fifteen white individuals in every hundred born. This conclusion is absurd, as every breeder knows. There is certainly something wrong with Yule's figures, for they do not accord with observation. In

reality, an error lies in the very first step of his calculation, which invalidates all that follows. He says, "The 100 pure individuals will give rise to dominant forms in the proportion of 50 pure to 50 hybrids." On the contrary, "pure" dominants bred *inter se* will produce only pure dominant offspring; but if they mate at random with any individuals of the entire 300, there are only two chances out of three that they will mate with *hybrid* dominants, which mating alone could yield "dominant forms in the proportion 50 pure to 50 hybrids." Yule accordingly estimates too low the proportion of dominant individuals in the various generations.

IV. RACE IMPROVEMENT BY SELECTION OF DESIRABLE OR BY ELIMINATION OF UNDESIRABLE INDIVIDUALS.

On the hypotheses, which I understand Yule to adopt, of random mating and equal fertility on the part of all individuals, 300 dominant forms, of which 100 are pure and 200 hybrid, will produce more than 88 per cent of dominant individuals, instead of 83 per cent as estimated by Yule. For if we suppose each class to consist of males and females in equal numbers, the chances are just twice as great that an individual will mate with a hybrid dominant, $A(B)$, as that it will mate with a pure dominant, A . Or, to put the matter in another way, there are, for each individual of the entire 300, 50 possible A mates, and 100 possible $A(B)$ mates. This makes the entire number of different matings possible: —

	$A.$	$A(B).$	$B.$
5,000 $A \times A$, yielding offspring	5,000		
20,000 $A \times A(B)$, yielding offspring	10,000	+ 10,000	
20,000 $A(B) \times A(B)$, yielding offspring	5,000	+ 10,000 + 5,000	
Total		20,000 + 20,000 + 5,000	

or 4 A : 4 $A(B)$: 1 B . It will be observed that §, or 88.8 per cent, of the offspring have the dominant form, being either A or $A(B)$ in character. Eliminating the one recessive individual, B , in each nine offspring, the parents of the next generation will consist of 4 A s (pure dominants) and 4 $A(B)$ s (hybrid dominants); that is, of equal numbers of individuals A and $A(B)$. The possible matings * in this case will be: —

* To simplify the calculation, it is well to remember that the numerical proportions of the various matings possible within a population are expressed by the square of that population. Knowing the nature and numerical proportions of the possible matings, one can quickly calculate the numerical proportions of the offspring. Thus, in a population consisting of equal numbers of individuals A and $A(B)$, the possible matings are expressed by the square of $A + A(B)$, or

	A.	$A(B)$.	B.
$2 A \times A$, yielding offspring	2		
$4 A \times A(B)$, yielding offspring	2	+	2
$2 A(B) \times A(B)$, yielding offspring	1	+	1
Total	$4\frac{1}{2}$	+	$3 + \frac{1}{2}$

or $9 A : 6 A(B) : 1 B$. The offspring in this generation are $\frac{15}{16}$, or 93.7 per cent, of the dominant form. Calculating in a similar way for the next four generations, we find that the proportion of dominant individuals steadily increases. The complete series for generations 1-8 following the cross between a pure A and a pure B is shown in Table III.

TABLE III.

RESULTS OF SELECTION FOR THE DOMINANT CHARACTER A IN THE VARIOUS GENERATIONS FOLLOWING A CROSS BETWEEN A
PURE A AND A PURE B .

Generation.	Parents.	Offspring.	Per cent A or $A(B)$.
1	$A + B$	$A(B)$	100
2	$A(B)$	$A + 2A(B) + B$	75
3	$A + 2A(B)$	$4A + 4A(B) + B$	88.8
4	$A + A(B)$	$9A + 6A(B) + B$	93.7
5	$3A + 2A(B)$	$16A + 8A(B) + B$	96
6	$2A + A(B)$	$25A + 10A(B) + B$	97.2
7	$5A + 2A(B)$	$36A + 12A(B) + B$	98
8	$3A + A(B)$	$49A + 14A(B) + B$	98.4

Inspection of the table will allow one to continue it to any desired extent.* Compare Diagram on p. 239, D.

$A^2 + 2A \cdot A(B) + A(B)^2$. Treating the progeny of each mating as equal to four, we have

	A.	$A(B)$.	B.
1 mating $A \times A$, yielding offspring	4		
2 matings $A \times A(B)$, yielding offspring	4	+	4
1 mating $A(B) \times A(B)$, yielding offspring	1	+	2
Total offspring	$9A + 6A(B) + B$		

* The percentage of dominant forms in the various generations may be quickly calculated by observing that it equals the series

$$\frac{1}{1} + \frac{(2)^2 - 1}{(2)^2} + \frac{(3)^2 - 1}{(3)^2} + \frac{(4)^2 - 1}{(4)^2} + \frac{(5)^2 - 1}{(5)^2} \text{ etc.}$$

From the foregoing considerations, we see that it is entirely possible for a breeder, under the conditions stated, practically to eliminate an undesirable recessive character, in a very few generations, *merely by not breeding from individuals which manifest that character*. This accords with experience. There is, however, a much quicker and surer way of accomplishing the desired result, namely, by selection of *pure* dominants only for breeding purposes. If a dominant individual, when bred to a recessive mate, has produced among two or more offspring no recessive individual, it is probable that the dominant is *pure*, and if mated to a similar individual will produce no recessive offspring in subsequent generations.

By means of a few preliminary breeding tests of individual animals or plants the breeder is thus enabled to establish a race of pure dominants as early as the second generation following a cross with recessives. A race of recessives which will breed true, may of course be established at any time by mating two recessive individuals. If the Galton-Pearson law were correct, neither of these things would be possible.

Suppose that the breeder, as is often the case, does not care to take the trouble to establish a perfectly pure race, being anxious to market large numbers of individuals as soon as possible. By merely weeding out the undesirable recessive individuals his race will steadily improve, as indicated by Table III and the diagram on p. 239, D. In the second generation following a cross between pure dominant and pure recessive individuals it will, as we have seen, consist of 75 per cent dominant individuals; in the next generation it will consist of 88.8 per cent dominants, and so on.

If the breeder eliminates recessives but once, namely, in the second generation following the cross, the series will be as follows:—

1st generation	100	% dominants
2d generation	75	"
3d generation	88.8	"
4th generation	88.8	"

etc., *ad infinitum*. If he eliminates recessives twice only, namely, in the second and third generations, the race will thereafter continue to contain 93.7 per cent dominant individuals, as follows:—

1st generation	100	% dominants
2d generation	75	"
3d generation	88.8	"
4th generation	93.7	"
5th generation	93.7	"

etc., *ad infinitum*. Similarly, if recessives are eliminated three times only, the race will be stable at 96 per cent dominants; and if four times, at 97.1 per cent dominants. In general, *as soon as selection is arrested the race remains stable at the degree of purity then attained*, provided of course that one form is as fertile as the other, and subject to no greater mortality.

Such is the law governing the transmission of a dimorphic condition within a race, or, to give the matter a practical bearing, we may call it

TABLE IV.

RESULTS OF SELECTION FOR THE CHARACTER *A* IN THE VARIOUS GENERATIONS FOLLOWING A CROSS BETWEEN A PURE *A* AND A PURE *B*.

Gener- ation.	When Dominance is Alternative between <i>A</i> and <i>B</i> .			When <i>A</i> is uni- formly Domi- nant over <i>B</i> .
	Parents.	Offspring.	Per cent <i>A</i> or <i>A(B)</i>	
1	<i>A + B</i>	<i>A(B) + B(A)</i>	50	100
2	<i>A(B)</i>	<i>A + A(B) + B(A) + B</i>	50	75
3	<i>A + A(B)</i>	$9A + 3A(B) + 3B(A) + B$	75	88.8
4	$8A + A(B)$	$49A + 7A(B) + 7B(A) + B$	87.5	93.7
5	$7A + A(B)$	$(15)^2A + 15A(B) + 15B(A) + B$	98.7	96
6	$15A + A(B)$	$(31)^2A + 31A(B) + 31B(A) + B$	96.8	97.2
7	$31A + A(B)$	$(63)^2A + 63A(B) + 63B(A) + B$	98.4	98
8	$63A + A(B)$	$(127)^2A + 127A(B) + 127B(A) + B$	99.2	98.4

the *law governing race improvement*, in cases of alternative inheritance, in which one of a pair of characters is uniformly dominant over the other. In cases in which dominance alternates between the two characters *A* and *B* (and such cases are probably commoner than is generally suspected) the process of race improvement by elimination of undesirable individuals progresses at first somewhat more slowly, but ultimately even more rapidly than in the case already discussed. A cross between *A* and *B* will, when dominance is alternative, yield offspring 50 per cent *A(B)*, 50 per cent *B(A)*. Selecting for *A*, that is, breeding only from *A(B)*s, the next generation will consist of equal numbers of forms

A, *A(B)*, *B(A)*, and *B* respectively, or once more 50 per cent individuals *A* in appearance. See Table IV. Selecting again for *A*, the parents for generation 3 will consist of equal numbers of individuals *A* and *A(B)* in character. Continuing the calculation in this way, we get the series of generations indicated in Table IV, and expressed graphically in the diagram on p. 239, *A*. For convenience in compari-

TABLE V.

CHANCES IN 100 OF ISOLATING A PURE *A* BY RANDOM SELECTION FROM INDIVIDUALS MANIFESTING THAT CHARACTER IN THE VARIOUS GENERATIONS FOLLOWING A CROSS BETWEEN A PURE *A* AND A PURE *B*.

Generation.	When Dominance is Alternative between <i>A</i> and <i>B</i> .*	When <i>A</i> is uniformly Dominant over <i>B</i> .†
1	0	0
2	50	33.3
3	75	50
4	87.5	60
5	93.7	66.6
6	96.8	71.4
7	98.4	75
8	99.2	77.7

son, there are also given in the last column of Table IV the percentages of *A* and *A(B)* individuals to be expected when *A* is uniformly dominant over *B*. Compare Table III. Inspection of Table IV will allow one to continue it to any desired extent.

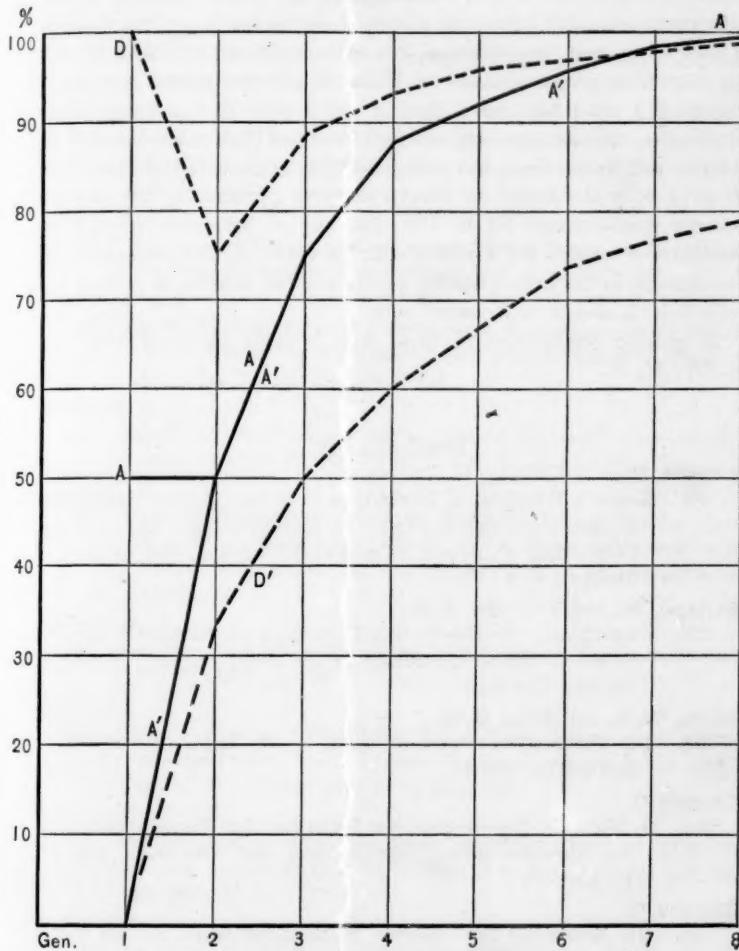
The same law governs arrest of selection in cases of alternative dominance, as in cases of uniform dominance of *A* over *B*. As soon as selection by elimination ceases, the race continues in the condition at that time attained, provided forms *A* and *B* are equally fertile and subject to the same mortality.

On the other hand, if the breeder has the patience to make individual breeding tests, and then to select for *pure* individuals on the basis

* These percentages equal the series 0, $\frac{1}{2}$, $\frac{2}{3}$, $\frac{3}{4}$, $\frac{4}{5}$, etc.

† These percentages equal the series 0, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{4}{15}$, etc.

DIAGRAM SHOWING THE PROGRESS OF SELECTION IN CASES OF ALTERNATIVE INHERITANCE.



A, Rate of Race Improvement by Elimination, Dominance being Alternative.

D, Same, Dominance being Uniform.

A', Chances in 100 of obtaining a Pure Individual, Dominance being Alternative.

D', Same, Dominance being Uniform.

of the tests made, immediate success in obtaining a pure race is assured, whether dominance be alternative or not. But if he selects for pure individuals quite at random, without breeding tests, his chances of success are considerably greater in a case of alternative dominance than in a case of uniform dominance of one character over the other, as will be clear from an examination of Table V. In the second generation following a cross between a pure *A* and a pure *B*, dominance being alternative, the chances are even that any *A* individual selected at random will breed true; and when individuals possessing the character *B* have been eliminated for three successive generations, the chances become approximately 94 in 100 that any *A* individual selected at random will breed true; whereas, when *A* uniformly dominates over *B*, the chances, in the corresponding generations, of securing a pure *A* are only 1 in 3, and 2 in 3 respectively.

A graphic presentation of these facts is made in the diagram on p. 239, *A'*, *D'*.

BIBLIOGRAPHY.

Bateson, W.

- :02. Mendel's Principles of Heredity, a Defence. With a Translation of Mendel's Original Papers on Hybridisation. xiv + 212 pp. Cambridge. [England. Contains bibliography and portrait of Mendel.]

Bateson, W., and Saunders, E. R.

- :02. Experimental Studies in the Physiology of Heredity. Reports to the Evolution Committee of the Royal Society. Report I. 160 pp. London.

Castle, W. E., and Allen, G. M.

- :03. The Heredity of Albinism. Proc. Amer. Acad. Arts and Sci., Vol. 38, pp. 603-622.

Correns, C.

- :01. G. Mendel's Regeln über das Verhalten der Nachkommenschaft der Rassenbastarde. Ber. deutsch. bot. Gesellsch., Bd. 18, pp. 158-168.

Correns, C.

- :01. Die Ergebnisse der neuesten Bastardforschungen für die Vererbungstheorie. Ber. deutsch. bot. Gesellsch., Bd. 19, Generalversammlungsheft, pp. 72-94.

Correns, C.

- :03. Ueber Bastardirungsversuche mit Mirabilis-Sippen. Erste Mittheilung. Ber. deutsch. bot. Gesellsch., Bd. 20, pp. 594-608.

Davenport, C. B.

:00. Review of von Guaita's Experiments in Breeding Mice. *Biol. Bull.*, Vol. 2, pp. 121-128.

Galton, F.

'89. *Natural Inheritance*. ix. + 259 pp., 16 figs. Macmillan and Co., London and New York.

Galton, F.

'97. The Average Contribution of each Several Ancestor to the Total Heritage of the Offspring. *Proc. Roy. Soc., London*, Vol. 61, pp. 401-413.

Guaita, G. von.

'98. Versuche mit Kreuzungen von verschiedenen Rassen des Hausmaus. *Ber. naturf. Gesellsch. zu Freiburg*, Bd. 10, pp. 317-332.

Guaita, G. von.

:00. Zweite Mittheilung über Versuche mit Kreuzungen von verschiedenen Rassen des Hausmaus. *Ber. naturf. Gesellsch. zu Freiburg*, Bd. 11, pp. 131-138, 3 Taf.

Hurst, C. C.

:02. Mendel's Principles applied to Orchid Hybrids. Reprint from *Jour. Roy. Hortic. Soc.*, Vol. 27, Pts. 2 and 3, 11 pp., 3 fig.

Hurst, C. C.

:03. Mendel's Principles applied to Wheat Hybrids. Reprint from *Jour. Roy. Hortic. Soc.*, Vol. 27, Pt. 4, 18 pp. [Contains Spillman's (:02) account of his experiments in hybridization of wheats.]

Mendel, G.

'66. Versuche über Pflanzenhybriden. *Verh. Naturf. Vereins in Brünn*, Bd. 4, Abh., pp. 3-47. [Translation in Bateson, :02.]

Mendel, G.

'70. Ueber einige aus künstlicher Befruchtung gewonnenen Hieracium-Bastarde. *Verh. Naturf. Vereins in Brünn*, Bd. 8, Abh., pp. 26-31. [Translation in Bateson, :02.]

Pearson, K.

'98. Mathematical Contributions to the Theory of Evolution. On the Law of Ancestral Heredity. *Proc. Roy. Soc., London*, Vol. 62, pp. 386-412.

Pearson, K.

:03. The Law of Ancestral Heredity. *Biometrika*, Vol. 2, Pt. 2, pp. 211-236.

Spillman, W. J.

:02. Quantitative Studies on the Transmission of Parental Characters to Hybrid Offspring. *Bull. 115, Office of Exp. Sta., U. S. Dept. Agric.*, pp. 88-98.

Spillman, W. J.

:02^a. Exceptions to Mendel's Law. *Science, N. S.*, Vol. 16, pp. 794-796.

Tschermak, E.

:00. Ueber künstliche Kreuzung bei *Pisum sativum*. *Zeitsch. f. landwirths. Versuchswesen in Oester.*, Jahrg. 3, pp. 465-555.

Tschermak, E.

:01. Weitere Beiträge über Verschiedenwerthigkeit der Merkmale bei Kreuzung von Erbsen und Bohnen. (Vorläufige Mittheilung.) *Ber deutsch. bot. Gesellsch.*, Bd. 19, pp. 35-51.

Tschermak, E.

:01^a. Ueber Zuchtung neuer Getreiderassen mittlest künstlicher Kreuzung. *Zeitsch. f. landwirths. Versuchswesen in Oester.*, Jahrg. 4, pp. 1029-?.

Tschermak, E.

:02. Ueber die gesetzmässige Gestaltungsweise der Mischlinge. (Fortgesetzte Studie an Erbsen und Bohnen.) Sonderabdruck aus *Zeitsch. f. landwirths. Versuchswesen in Oester.*, Jahrg. 5, 81 pp., 1 Taf.

Tschermak, E.

:02^a. Der gegenwärtige Stand der Mendel'schen Lehre und die Arbeiten von W. Bateson. Sonderabdruck aus *Zeitsch. f. landwirths. Versuchswesen in Oester.*, Jahrg. 3, 28 pp.

Vernon, H. M.

:03. Variation in Animals and Plants. ix. + 415 pp. Henry Holt and Co., N. Y.

Vries, H. de.

:00. Sur la loi de disjonction des hybrides. *Compt. Rend.*, Paris, Tom. 130, pp. 835-847.

Vries, H. de.

:01-03. Die Mutationstheorie. Bd. 1, xii. + 648 pp. 181 Text fig., 8 Taf.; Bd. 2, xiv + 752 pp., 159 Text fig., 2 Taf. Veit & Co., Leipzig.

Webber, H. J.

:00. Xenia, or the Immediate Effect of Pollen, in Maize. *Bull. No. 22, Division of Veg. Physiol. and Pathol.*, U. S. Dept. Agric., Washington, D. C., 44 pp., 4 pl.

Yule, G. U.

:02. Mendel's Laws and their Probable Relations to Intra-racial Heredity. *The New Phytologist*, Vol. 1, pp. 193-207 and 222-237.

